

## WIND DISPERSAL OF SOME NORTH AMERICAN SPECIES OF *ANDROPOGON* (GRAMINEAE)

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**Abstract:** The plumed diaspores of the genus *Andropogon* are wind-dispersed. The dispersibility of Andropogons helps account for their success as colonizers both in their infestation of appropriate sites and their spread to newly available sites. The wind may also be responsible for the long-distance dispersal of *A. bicornis* L. from the Caribbean to southern Florida. This is the first record of this widespread New World taxon in the United States.

Many species of the cosmopolitan genus *Andropogon* are remarkably successful colonizers. Wherever there is full sun and in all but the poorest and driest of soils, they rapidly form large, dense populations. Some species usually grow away from frequent disturbance of the habitat by man and rely upon fire and other natural phenomena for an open canopy. Others are of limited range in man-made habitats like roadsides and old fields. The commonest species, such as *A. virginicus* L., tend to dominate all other vegetation in early stages of secondary succession (Keever, 1950; Golley, 1965; Bazzaz, 1975). The colonizing success of Andropogons comes, at least in part, from their dispersibility.

Andropogons flower at the end of the first or second year of growth. The number of flowers per stem varies from as few as 100 in *Andropogon gyrans* Ashe (long incorrectly known as *A. elliotii* Chapman) to as many as 10,000 in *A. glomeratus* (Walter) B.S.P. The number of stems per individual may be as high as 60. Fruit set depends upon the favorability of the habitat for growth, the extent of insect predation and other natural adversities (e.g. infestation by the smut *Sorosporium*), which vary considerably and can reduce fruit set greatly as in other grasses (Roos & Quinn, 1977). The caryopsis is small (1–4 mm long and less than 0.5 mm in diameter) and light (0.2–0.9 mg). It remains within the spikelet after maturation. Dispersal of the fruit begins with the disarticulation of the racemes of spikelets into units (Figure 1) consisting of the internode of the rachis of the raceme, one spikelet (bearing one fruit), and a pedicel bearing a second spikelet, which is either vestigial or stami-

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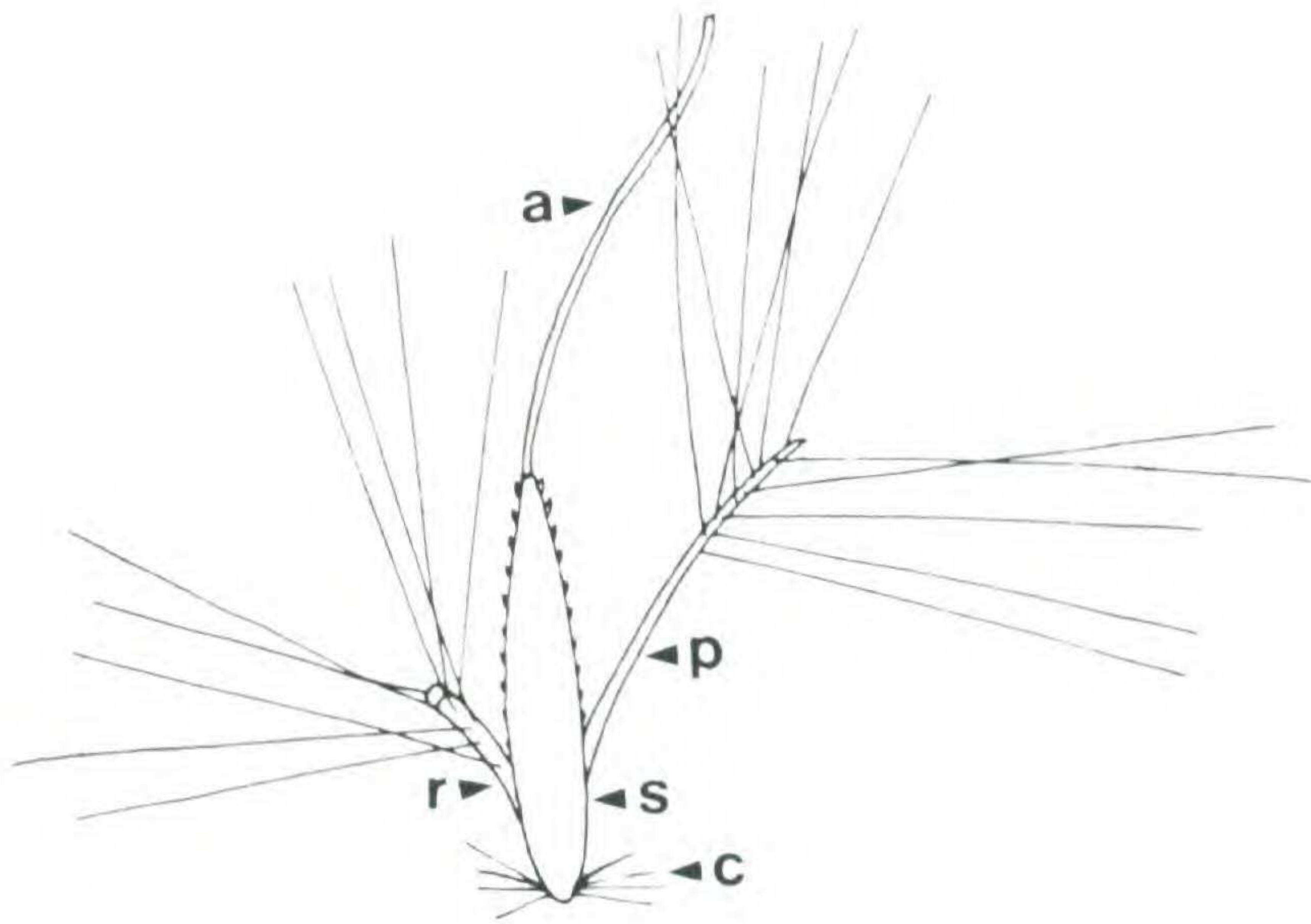


Figure 1. **Diaspore of *Andropogon glomeratus* var. *pumilus***, many hairs of callus, pedicel and rachis internode omitted. a – awn (only base shown), c – callus hairs, p – pedicel (pedicelled spikelet completely suppressed), r – rachis internode, s – spikelet (showing lower glume with marginal prickly hairs).

nate and caducous. The spikelet itself is glabrous except for short (less than 5 mm) hairs on the callus, but the rachis internode and pedicel of many species bear long hairs (1–13 mm, especially toward the apex). These hairs, as well as the rachis internode and pedicel spread horizontally at maturity and, when the atmosphere is dry, form a plume. This unit of dispersal, or diaspore, is then ready to be carried away by the wind. The dispersal distance of plumed diaspores increases as height of release of the diaspores, wind velocity, and convection (vertical air movement) increase. Dispersal decreases as terminal or fall velocity of the diaspore, density and height of surrounding vegetation, and atmospheric humidity and precipitation increase. Diaspores released from a higher point will take longer to fall to the ground and will be subjected to the atmospheric forces which may carry them about for a longer time. Doubling the height of release will double the dispersal distance in a constant wind and convection velocity (Sheldon & Burrows, 1973). The arrangement of the diaspores and hence their height of release is determined by the shape of the inflorescence. In *Andropogon virginicus* the spikelets are more or less evenly spaced over the upper



two-thirds of the plant. The spikelets of *A. bicornis* L. and *A. glomeratus* in contrast, are usually densely clustered toward the top of the stems. The average height of release of diaspores from the latter species is greater than from the former.

The terminal velocity of the diaspores of four species of *Andropogon* and two other species have been computed (Table 1). *Taraxacum officinale* Weber is included as a commonly known reference point. The value obtained here is close to the value (35.7 cm/sec) determined by Sheldon and Burrows (1973). Confidence in the biological importance of these mean values lies in their reproducibility (compare the values for two different plants of *Andropogon gyrans* obtained on different days) and apparent genetic base (compare the two populations of *A. longiberbis* Hackel). The terminal velocity of an object reflects its coefficient of aerodynamic drag. The lower the terminal velocity the greater is the force opposing the acceleration due to gravity. That the main source of the aerodynamic drag is the plume of *Andropogon* diaspores is shown by their performance after the hairy rachis internode and pedicel have been removed. The mean times required to fall through two m by the intact diaspores of *A. virginicus* and *A. longiberbis* (Gilchrist County population) are 6.1 and 5.4 seconds respectively. After the rachis internode and pedicel have been removed, the fall times are 1.0 and 1.2 seconds respectively. In these species there does not appear to be any strong relationship between terminal velocity and weight of the diaspores. The most important factors are the length and density of hairs on the rachis internode and pedicel.

The diaspore of *Schizachyrium scoparium* (Michx.) Nash (*Andropogon scoparius* Michx.) resembles that of *Andropogons* in structure. The shortness of the hairs on the rachis internode and pedicel (2–4 mm long) accounts for its relatively high terminal velocity (Table 1).

If the only movement of the air is constant and parallel to the ground at, for example, 150 cm/sec (5.4 km/hr), a diaspore of *Andropogon glomeratus* released from 100 cm above the ground will travel 750 cm away from the plant before reaching the ground (assuming the diaspore moves at the same velocity as the wind). If there is any convection, the rate of fall of the diaspore will be reduced and its potential dispersal distance increased. If the ratio of convection velocity to terminal velocity is greater than or equal to one, there will be no downward movement of the diaspore, and it



Table 1. Terminal velocity<sup>a</sup> ( $\bar{x} \pm S.D.$ ) and weight<sup>b</sup> of plumed diaspores of several species. (N = 30)

Taxon Collector, number State, County	Terminal velocity (cm/sec)	Weight (mg) mean
<i>Andropogon virginicus</i> Campbell, 3782 Florida, Jackson	32.3 ± 4.6	0.35
<i>A. glomeratus</i> var. <i>pumilus</i> Vasey Campbell, 3739 Florida, Lee	20.1 ± 1.8	0.32
<i>A. gyrans</i> plant I Campbell, 3872 plant II Florida, Jackson	26.9 ± 2.7 29.8 ± 3.3	— 0.75
<i>A. longiberbis</i> Campbell, 3910 Florida, Gilchrist	37.8 ± 4.5	0.65
<i>A. longiberbis</i> Campbell, 3734 Florida, Dade	41.3 ± 6	—
<i>Schizachyrium scoparium</i> V. L. Cory, 11,348 Texas, Galveston	101 <sup>c</sup> ± 12	0.75–0.98 <sup>d</sup>
<i>Taraxacum officinale</i> Campbell Massachusetts, Middlesex	31 ± 6.2	—

<sup>a</sup>In all cases except *Schizachyrium scoparium* (see note c) the measurements of terminal velocity were made by dropping the diaspores in still air from about 2 dm above a line two m above the floor. A stop watch was started as the diaspore passed through the two meter height and stopped when it reached the floor. It appeared that all these diaspores reached terminal velocity rapidly, before reaching the two meter line. Sheldon and Burrows (1973) showed that plumed diaspores of the Compositae with terminal velocities of the same range as these reached terminal velocity quickly.

<sup>b</sup>Mean weight was determined by weighing 20 diaspores together and dividing the total by 20.

<sup>c</sup>Terminal velocity determined by dropping diaspores from two and one m separately and constructing a graph of height of release against time of fall. The slope of the line of the two data points is the terminal velocity (Sheldon & Burrows, 1973). The value given here is near that recorded for the same species (91 cm/sec) by Rabinowitz & Rapp (1981).

<sup>d</sup>From Roos and Quinn, 1977.



could be dispersed an infinite distance on the slightest breeze (Burrows, 1973).

In the Compositae, the pappus, which forms the plume, is sensitive to humidity (Sheldon & Burrows, 1973). At high humidities the pappus closes and is thereby protected from damage by raindrops and less likely to be released from the plant when raindrops could increase the downward movement of the diaspores. *Andropogon* diaspores are also hygroscopic. Diaspores of *Andropogon gyrans* suspended over water in a closed container radically change their configuration. The rachis internode, pedicel, and their many hairs quickly become tightly appressed to the spikelet. Although their terminal velocity was not determined in this condition, it is assumed that it would be about the same as a spikelet without rachis internode and pedicel. When these diaspores were placed under a lamp, the rachis internode, pedicel, and hairs spread to their horizontal position in a few seconds.

There are two aspects to the dispersal of a colonizing group. First, rapid spread in a local area which is edaphically and otherwise appropriate is the *sine qua non* of colonization. Observations of *Andropogon* dispersal in the eastern United States clearly indicate that the density of diaspores falls rapidly away from the plant. Dispersal appears to follow the pattern of *Senecio jacobaea* (Compositae) in which 60% of the plumed diaspores fell at the base of the plant, only 0.39% travelled beyond 4.6 m from the edge of the plants, 0.08% beyond 9 m, 0.02% beyond 18 m, and 0.005% greater than 36 m from the plot containing the plants (Harper, 1977).

Some habitats, like roadsides, may be more or less continuous, but most sites colonized by *Andropogons*, like fields, are discontinuous. Hence the second aspect of dispersal in connection with colonization is the transport of diaspores away from one locality to another suitable one some distance away. As Harper (1977) points out, "successional species are doomed in their present habitats, and their continued survival depends on escape and establishment elsewhere." The general process of colonization, then, is like that of Composites with specialized mechanisms for wind dispersal in which there are "isolated individuals over a great distance which may subsequently act as foci for new infections".

Under normal atmospheric conditions dispersal of diaspores away from the population to a distant and suitable new site may be a rather unlikely event. Long-distance dispersal becomes a greater



likelihood in extreme weather conditions such as hurricanes, tropical storms, and thunderstorms. From 1885 to 1971 inclusive, 160 tropical storms entered or significantly affected Florida (Anon, 1974). A little over half of these were of hurricane intensity (winds greater than 74 mph). The frequency of occurrence of hurricane force winds in any given year varies considerably: one in six around Miami, one in twenty-five in Tampa, one in eight in Tallahassee, and one in one hundred in Jacksonville, the least affected region in the state (Anon, 1974). Florida is the most strongly hit state in the southern United States. The usual hurricane tracks after passing through Florida — either to the northeast along the Atlantic Coastal Plain, or to the west into the Gulf of Mexico (Gentry, 1974) — pass over the center of greatest diversity of species of *Andropogon* in the United States and the area of their greatest prominence in the overall flora.

The tropical storm season of eastern North America overlaps with the period of diaspore dissemination in *Andropogon*. The average frequency of tropical cyclones (winds 39–73 mph) and hurricane peaks from August to October (Dunn & Miller, 1960). There is an average of 1.5, 2.6, and 1.9 tropical storms in each of these months respectively and 0.9, 1.6, and 0.8 hurricanes per month in the North Atlantic region in these three months respectively. *Andropogon* diaspores mature in late August, September, and especially October and November. As pointed out earlier, the dispersal capacity of the diaspores falls markedly when humidity is high. So the diaspores must be picked up by winds which are relatively dry (or very powerful). Once the diaspore is inside a storm itself, it is likely to be carried for a great distance.

Thunderstorms, though less powerful and more local, occur frequently enough to be potentially important modes of dispersal for *Andropogon* diaspores.

There is no direct evidence of the extent to which these diaspores are transported by storms. However, there is one possible example of long-distance dispersal. *Andropogon bicornis* is a common species of South and Central America and the West Indies. It has never been reported for the United States, and I have never seen it in my field work in South Florida. There is one specimen of this plant collected by F. C. Craighead in northern Monroe County in October of 1962 (deposited in the herbarium of the Fairchild Tropical Garden in Miami, Florida). It was identified as *A. floridanus*



Scribner, but the lack of awns and the conspicuous, staminate pedicelled spikelets leave no question of its being *A. bicornis*. It is possible that it was transported from the West Indies during Hurricane Donna in 1960. This was the most powerful hurricane in Florida's history, and its track passed within 30 miles of the site where Craighead found the plant. The nearest known localities of *A. bicornis* are in Cuba, over 300 km from Craighead's collecting site. Long-distance wind dispersal is also suspected in another genus of the Andropogoneae, *Bothriochloa* Kuntze, in which 15 of the 18 New World Species show major disjunctions between North and South America (Allred, 1981). After the diaspore becomes established following long-distance dispersal it must reproduce itself if the new site is to be colonized. The capacity for apomictic seed production has not been reported for *Andropogon* sensu stricto (Connor, 1979; Campbell, 1983). Most North American Andropogons are cespitose, so colonization depends upon sexual seed production. If these plants were self-incompatible, a second genotype would have to be present within the range of pollen dispersal for fertilization and seed production to be effected. The probability of two plants of differing genotypes arriving at the same place within one life span is much less than that of the establishment of a single individual. The fact that most North American Andropogons (and certainly the most vigorous colonizing species) are self-compatible and frequently cleistogamous (Campbell, 1982) increases the likelihood of the effectiveness of long-distance dispersal (Baker, 1953).

#### ACKNOWLEDGMENTS

R. C. Rollins, R. M. Tryon, and C. E. Wood, Jr. read an earlier draft. This work was supported by grants from the Anderson and Fernald Funds of Harvard University, the National Science Foundation (DEB 77-17317), and the Rutgers University Research Council (07-2200).

#### LITERATURE CITED

- ALLRED, K. 1981. Cousins to the South: Amphitropical disjunctions in *Bothriochloa* (Graminae). Abstract from Bot. Soc. Amer. meetings, Bloomington, Indiana.
- ANON. 1979. Climates of the States. 2 vols. Officials of the National Oceanic and Atmospheric Administration, U.S. Dept. of Commerce. Water Information Center, Inc. New York.



- BAKER, H. G. 1953. Race formation and reproductive effort in flowering plants. *Symp. Soc. Exptl. Biol.* **7**: 114–143.
- BAZZAZ, F. A. 1975. Plant species diversity in old-field successional ecosystems in Southern Illinois. *Ecology* **56**: 485–488.
- BURROWS, F. M. 1973. Calculation of the primary trajectories of plumed seeds in steady winds with variable convection. *New Phytol.* **72**: 647–664.
- CAMPBELL, C. S. 1982. Cleistogamy in *Andropogon* (Gramineae). *Amer. J. Bot.* **69**: 1649–1658.
- . 1983. Systematics of the *Andropogon virginicus* complex (Gramineae). *J. Arn. Arb.* (In press).
- CONNOR, H. E. 1979. Breeding systems in grasses: a survey. *New Zealand J. Bot.* **17**: 547–574.
- DUNN, G. E., & B. I. MILLER. 1960. Atlantic hurricanes. Louisiana State University Press. 326 pp.
- GENTRY, R. C. 1974. Hurricanes in South Florida. p. 73–81 *In*: Gleason, P. J. (ed.). *Environments of South Florida: past and present*. Memoir **2**, Miami Geological Society. 452 pp.
- GOLLEY, F. B. 1965. Structure and function of an old-field broomsedge community. *Ecol. Monogr.* **35**: 113–137.
- HARPER, J. L. 1977. *Population biology of plants*. Academic Press. London. 892 pp.
- KEEVER, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. *Ecol. Monogr.* **20**: 229–250.
- RABINOWITZ, D., & J. K. RAPP. 1981. Dispersal abilities of seven sparse and common grasses from a Missouri prairie. *Amer. J. Bot.* **68**: 616–624.
- ROOS, F. J., & J. A. QUINN. 1977. Phenology and reproductive allocation in *Andropogon scoparius* (Gramineae) populations in communities of different successional stages. *Amer. J. Bot.* **64**: 535–540.
- SHELDON, J. C., & F. M. BURROWS. 1973. The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. *New Phytol.* **72**: 665–675.

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